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A NEW GENUS AND SPECIES OF PHREATIC AMPHIPOD (CRUSTACEA: AMPHIPODA) BELONGING IN THE "CHILTONIA" GENERIC GROUP, FROM DALHOUSIE SPRINGS, SOUTH AUSTRALIA

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Summary

ZEIDLER, W. (1991) A new genus and species of phreatic amphipod (Crustacea: Amphipoda) belonging in the "chiltonia" generic group, from Dalhousie Springs, South Australia. *Trans. R. Soc. S. Aust.* 115(4), 177-187, 29 November, 1991.

A freshwater amphipod *Phreatochiltonia anophthalma* gen. et sp. nov. is described and illustrated. It is endemic to a few small, cold, artesian springs amongst the Dalhousie Springs complex in the north of South Australia. Unlike species of the closely related genus *Austrochiltonia* the new species seems to be subterranean in habit, is completely white, lacks eyes, and coxa 4 is without a clearly defined posterior excavation.

"Chiltonias" generally are considered to be more closely allied to the Hyalellidae than the Ceinidae, and thus transference of chiltonid genera (subfamily Chiltoniinae) to Hyalellidae is recommended.

KEY WORDS: *Phreatochiltonia anophthalma* gen. et sp. nov., new species, amphipod, artesian springs, Australia, taxonomy.

Introduction

Recent studies of the mound spring fauna of the Great Artesian Basin in South Australia have revealed a diverse endemic fauna (Ponder 1985, 1986; Ponder *et al.* 1989; Zeidler & Ponder 1989). This fauna, components of which are endemic to certain springs or spring groups, is dominated by hydrobiid molluscs (Ponder *et al.* 1989) and crustaceans including amphipods of the genus *Austrochiltonia* Hurley, 1959 (not *Afrochiltonia* K. H. Barnard, 1955 - see Zeidler 1988).

During a recent survey of the fauna of Dalhousie Springs in the extreme north of South Australia (Zeidler & Ponder 1989), we discovered several populations of an undescribed amphipod similar to the *Austrochiltonia* species commonly found in other mound springs, but without eyes. A detailed examination of this species has revealed several characters which preclude it from *Austrochiltonia* or any other allied genus. I therefore propose a new genus to accommodate this new species.

Chiltonias (subfamily Chiltoniinae) also occur in New Zealand (*Chiltonia* Stebbing, 1899) and South Africa (*Afrochiltonia*), but until now no phreatic species have been described, although Williams (1986) reports the probable occurrence of some in Western Australia, from springs and caves near Perth.

The familial placement of chiltonias is briefly reassessed and they are considered to be more closely allied to the Hyalellidae than the Ceinidae, and thus transference of chiltonid genera to Hyalellidae is recommended.

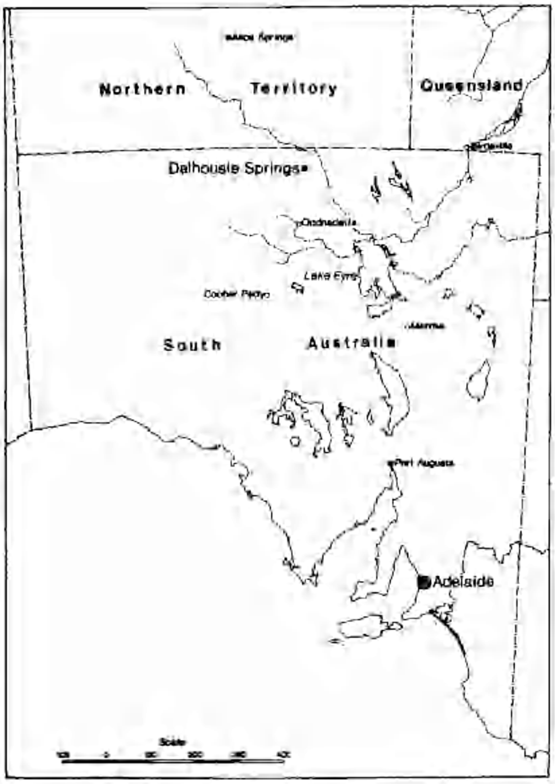

Fig. 1. Location of Dalhousie Springs, South Australia.

Materials and Methods

Specimens were collected from five rather small, relatively cool, seeps amongst the Dalhousie Springs complex (Fig. 1). The springs are coded following Zeidler & Ponder (1989) (see Fig. 2). Animals were

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TABLE 1. *Temperature measurements, at time of collection, for habitats of* Phreatochiltonia anophthalma *sp. nov. and physicochemical data (from Smith 1989) for nearby springs (measured as close as possible to source).*

Habitat	Temp. Air °C	Temp. Water °C	Nearest Spring	Field Chemistry					Lab. Chem.	
				Temp. °C	Cond. 25°C Siemens	TDS mg/L	PH	D.O. ppm	TDS mg/L	PH
Cb1	20	20	None	–	–	–	–	–	–	–
Db4a	22.5	22.5	Db3	35	1500	830	7.1	0.6	901	7.6
Nth of E2	–	–	E2	36	1600	890	7.3	1.9	–	–
E8	22	23	E1	29	1480	820	7.7	7.5	930	7.5
Ga4	22	17	Ga1	32	2100	1180	7.1	1.0	1220	7.0
″			Ga3	34	2120	1190	7.1	2.1	1275	7.3

collected with a small hand sieve or picked off plant debris with forceps, and once, when no surface water was present (at Cb1), two specimens were collected using a household cotton mop placed in a pit dug to water level (approx. 1m). A total of 676 specimens (366 ♀♀, 263 ♂♂, 47 juveniles) were collected and examined.

Physicochemical data for the sites sampled are unavailable because too little surface water was present for meaningful analysis. However, air and water temperatures were measured at the time of collection, and these and physicochemical data for nearby springs are given in Table 1.

Material reported here is deposited in the South Australian Museum, Adelaide (SAM), and the Australian Museum, Sydney (AM). All specimens are preserved in 75% alcohol or 2% formaldehyde/propylene glycol solution. Of the types, only the holotype, allotype and one paratype ♂ have been dissected (partially), with appendages removed from the left hand side of the animal unless indicated otherwise. Dissected appendages are preserved with the carcass or, in the case of the holotype, the mouthparts, pleopods 1-3, and the uropods and telson are mounted in poly-vinyl lactophenol on a microscope slide.

Specimen length is measured along a lateral parabolic line drawn from the anterior extremity of the head through the middle of the body to the posterior limit of the telson.

The thoracic limbs are referred to as gnathopod 1 and 2 followed by pereopods 3-7 to avoid confusion. Size comparisons of gnathopods exclude the coxa and dactyl, and of the pereopods, the coxa, with articles being measured along the middle.

The following abbreviations are used in the text. A1 = first antenna; G1 = gnathopod 1 (first pereopod); G2 = gnathopod 2 (second pereopod); P3-7 = pereopods 3-7; U1-3 = uropods 1-3.

Systematics

Phreatochiltonia gen. et sp. nov.

Type species: *Phreatochiltonia anophthalma* sp. nov.

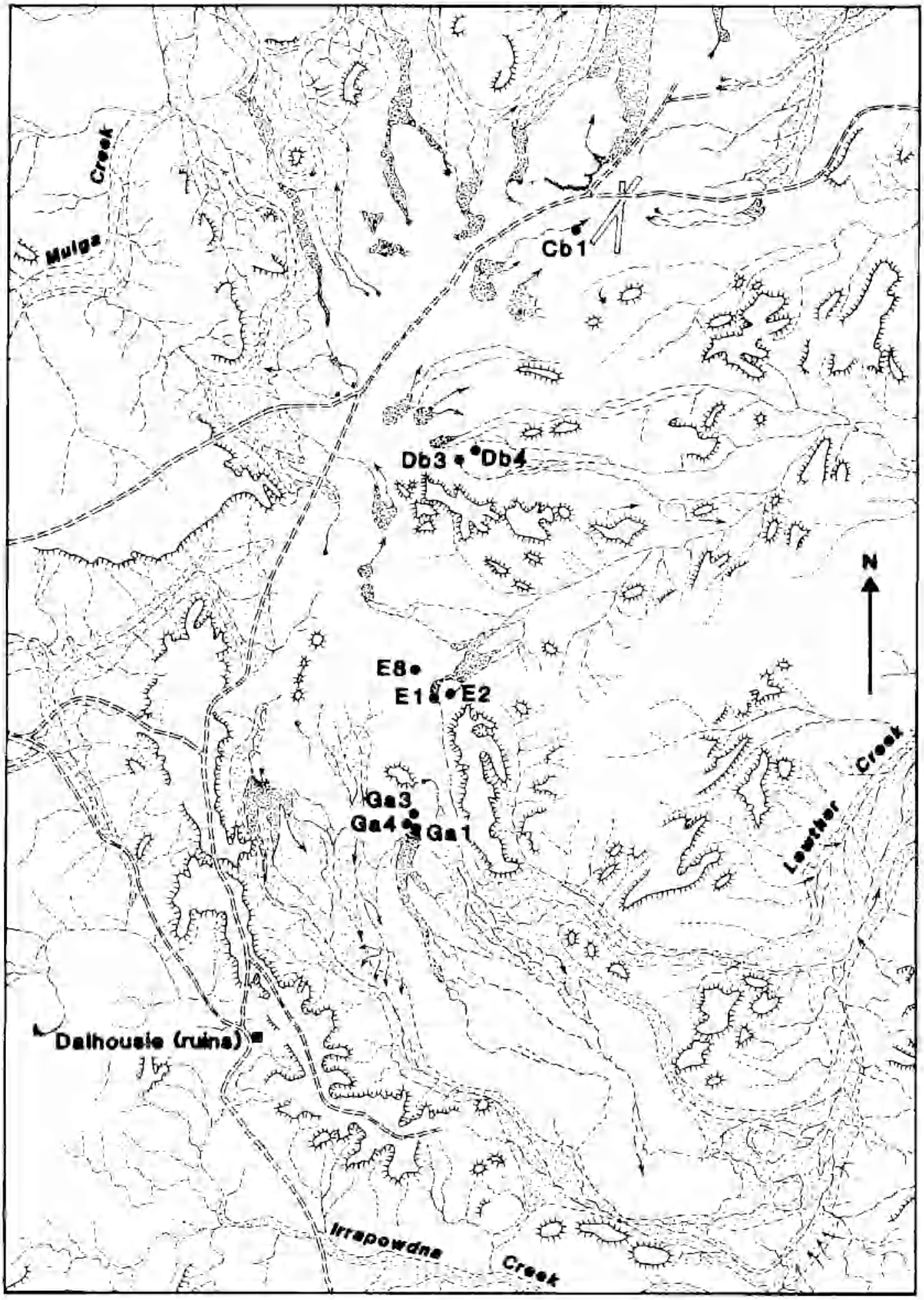
Diagnostic definition: Males about ¾ size of females. Eyes absent. Antenna 1 longer than antenna 2, about ⅓ body length; ventral aesthetasc at base of distal three or four (rarely five) flagellar articles. Antenna 2, length almost 0.7× antenna 1; gland cone pressed against head, not readily visible laterally. Maxilla 1 without palp, notched at palp's normal position. Coxae 1-4 deep. Coxa 4 without well-defined posterior excavation; maximum width greater than length (up to 1.25× in female). Gnathopods 1 and 2 subchelate in both sexes; article 6 of gnathopod 2 enlarged in male. Pereopods slender; pereopod 5 distinctly shorter than pereopod 4; pereopod 6 distinctly shorter than pereopod 7. Pleopods unmodified in both sexes. Uropod 3 with single ramus or ramus absent. Telson entire, subrectangular with slightly concave distal margin. Coxal gills on gnathopod 2 to pereopod 6. Oostegites on gnathopod 2 to pereopod 5.

Etymology: The generic name, *Phreatochiltonia*, refers to the phreatic habit of the type species, and acknowledges its similarity to *Austrochiltonia*.

Systematic status of *Phreatochiltonia* gen. nov. and other chiltonid genera.

The new genus clearly belongs to the "chiltonia" generic group (subfamily Chiltoniinae). It is most similar to *Austrochiltonia*, but is readily distinguished from this and the other two chiltonid genera (*Chiltonia* and *Afrochiltonia*) by the following characters; 1) the phreatic habit; 2) the complete lack of eyes; 3) coxa 4 is without well-

Fig. 2. Dalhousie Springs complex showing sites (coded) from which *Phreatochiltonia anophthalma* gen. et sp. nov., has been collected and adjacent springs (referred to in Table 1). Scale = 1:100,000. (Other springs, swamps from springs and creek beds are stippled.) ⟶


Mulga
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Cb1
Db3
Db4
E8
E1
E2
Ga3
Ga4
Ga1
N
Lowther
Creek
Dalhousie (ruins)
Irrapowdna
Creek

defined posterior excavation, and 4) pereopod 5 is distinctly shorter than pereopod 4.

The current familial placement of the chiltonid genera is uncertain. Barnard (1972a) originally placed the chiltonias in his new family, Ceinidae (Barnard 1972b). Bousfield (1982) however, includes the chiltonias in the Hyalellidae, in a brief synopsis of the family, but gives no reasons for this rearrangement; it has thus been ignored or not been accepted (e.g. Zeidler 1988; Barnard & Barnard 1990).

The inclusion of chiltonias in the family Ceinidae by Barnard (1972a) is not altogether satisfactory. They differ from *Ceina* Della Valle, 1893, the type genus, in several key characters; *Ceina* has an aberrant mandibular molar consisting of a long, conical, non-triturative protuberance, and a flat, distinctly cleft telson, whereas chiltonias have a relatively large, triturative mandibular molar, and the telson is curved over the anus and is not cleft except in *Chiltonia mihiwaka* (Chilton, 1898) (for distal ¼). Chiltonias appear to have more in common with *Hyalella* Smith, 1874 and *Allorchestes* Dana, 1849, particularly with respect to the mandible, uropod 3 and the telson. I therefore recommend that the chiltonias, *Afrochiltonia*, *Austrochiltonia*, *Chiltonia* and *Phreatochiltonia* gen. nov., be placed in the family Hyalellidae together with *Allorchestes*, *Hyalella* and *Parhyalella* Kunkel, 1910, subject to a thorough revision of the hyalellids.

Phreatochiltonia anophthalma sp. nov.

FIGS 3–35

Austrochiltonia sp. Zeidler, 1989, pp. 83–84, fig. 12.1A.

Holotype: SAM C4228. Adult male, South Australia, Dalhousie Springs, from small seep of spring Db4 (Db4a), 26°26′49″S 135°29′15″E, W. Zeidler & K. L. Gowlett-Holmes, 9.vi.1985.

Allotype: SAM C4229. Adult female. Collected with holotype.

Paratypes: All with same collection data as holotype, except AM specimens collected by W. F. Ponder & D. Winn. AM P40445, 3♀♀, 2♂♂. SAM C4230, 1♂ 3.1 mm. SAM C4231, 136♀♀ (19 ovigerous), 102♂♂, 39 juveniles.

Other material examined: All from Dalhousie Springs area (Fig. 2). AM P40446, 1♀, spring Cb1, 26°25′16″S 135°29′52″E, from shallow pool at top of mound, W. F. Ponder, 30.v.1983. SAM C4232, 2♀♀, spring Cb1, from mop trap in pit dug to water level (approx. 1m), W. Zeidler, 14.vi.1985. SAM C4233, 1♂, from small seep of spring Db4 (Db4b), 26°26′49″S 135°29′15″E, W. Zeidler & K. L. Gowlett-Holmes, 9.vi.1985. SAM C4234, 2♀♀ (both ovigerous), from small seep amongst trees (*Melaleuca glomerata*) just north of spring E2, 26°28′30″S 135°29′05″E, W. Zeidler & K. L. Gowlett-Holmes, 8.vi.1985. AM P40447, 23♀♀ (one ovigerous), 38♂♂, spring E8, 26°28′21″S 135°28′52″E, from small seep on north side of mound, W. F. Ponder & D. Winn, 13.vi.1985. SAM C4235, 96♀♀ (33 ovigerous), 92♂♂, spring E8, from small seep on north side of mound, W. Zeidler & K. L. Gowlett-Holmes, 10.vi.1985. AM P40448, 27♀♀ (one ovigerous), 6♂♂, spring Ga4, 26°29′23″S 135°29′10″E, from small seep, W. F. Ponder & D. Winn, 4.vi.1985. SAM C4236, 75♀♀ (20 ovigerous), 20♂♂, 8 juveniles, spring Ga4, from small seep, W. Zeidler & K. L. Gowlett-Holmes, 8.vi.1985.

Definition: As for genus with the following additions. Specimens entirely white, relatively small, body length of females up to 4.4 mm, males up to 3.2 mm; relatively robust. Coxal plates 1–3 slightly wider proximally than distally. Oostegites relatively large, that on coxal plate 2 almost as long as gnathopod 2. Uropod 3 a single article.

Description of holotype: Male 2.9 mm (Fig. 3). Coxal gills sausage shaped, present from G2 to P6.

Head about as long as deep, length equivalent to first 1–5 pereonites.

Antenna 1 (Fig. 4) about 3× head length; article 1 of peduncle, width 0.6× length and slightly more than 1.5× length article 2, article 3 slightly shorter than article 2; flagellum length almost 1.5× peduncle, of nine articles with one ventral aesthetasc at base of each of last four articles.

Antenna 2 (Fig. 5), article 1 of peduncle as long as wide, article 2 almost twice as long as wide, twice length article 1 and about ⅔ length article 3; flagellum only slightly longer than peduncle, of seven articles.

Upper lip (Fig. 11): slightly wider than long, apically rounded, bearing numerous short setae distally.

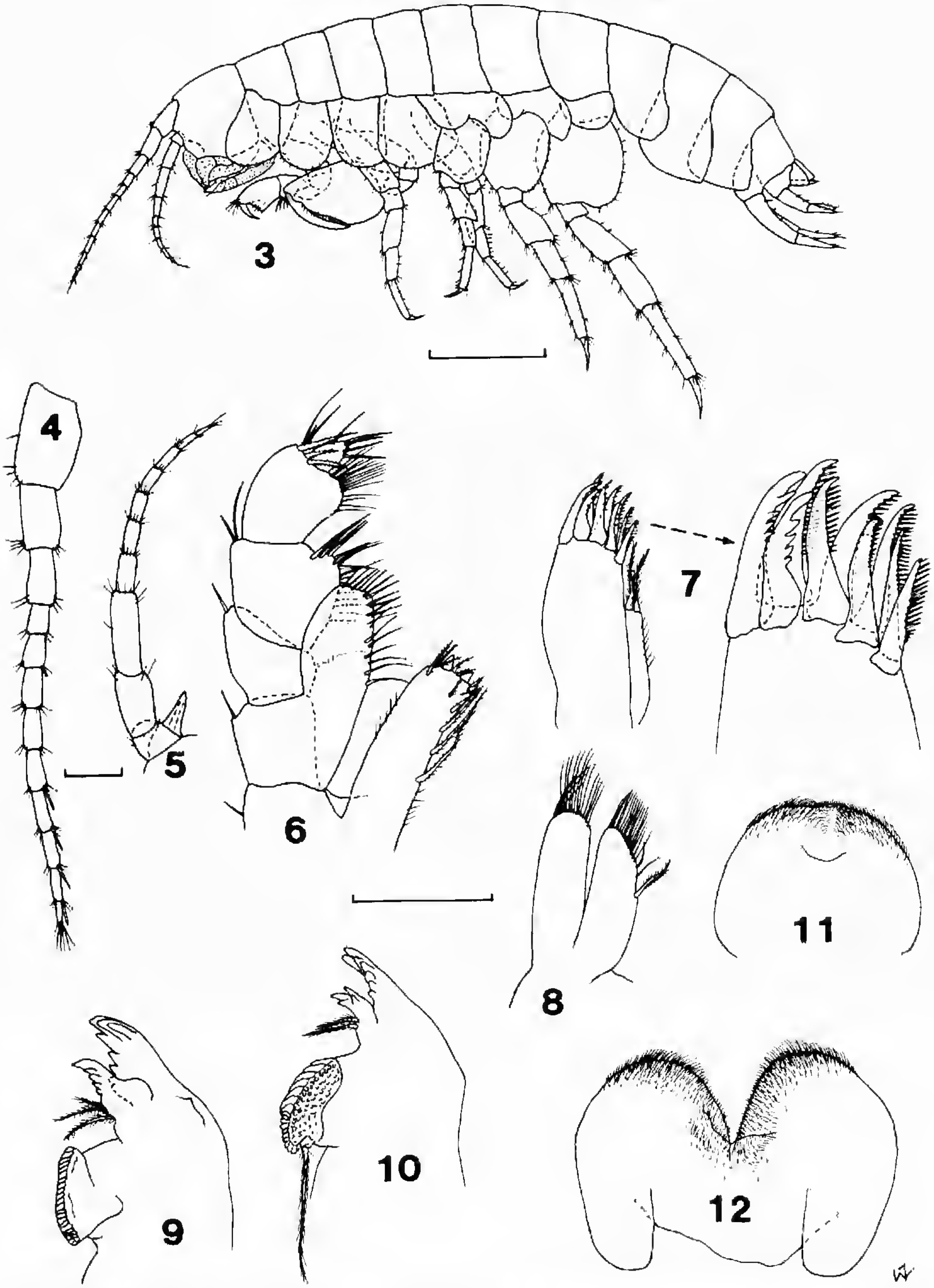
Lower lip (Fig. 12): inner lobes vestigial, outer lobes subovate with setose distal and inner margins.

Mandibles without palp: left (Fig. 9) with incisor of seven teeth plus one tiny protuberance, lacina mobilis of five teeth, spine row of three feathered spines, molar triturative; right (Fig. 10) with incisor of seven teeth, lacina mobilis of four teeth, spine row of two feathered spines, molar triturative with one long feathered seta.

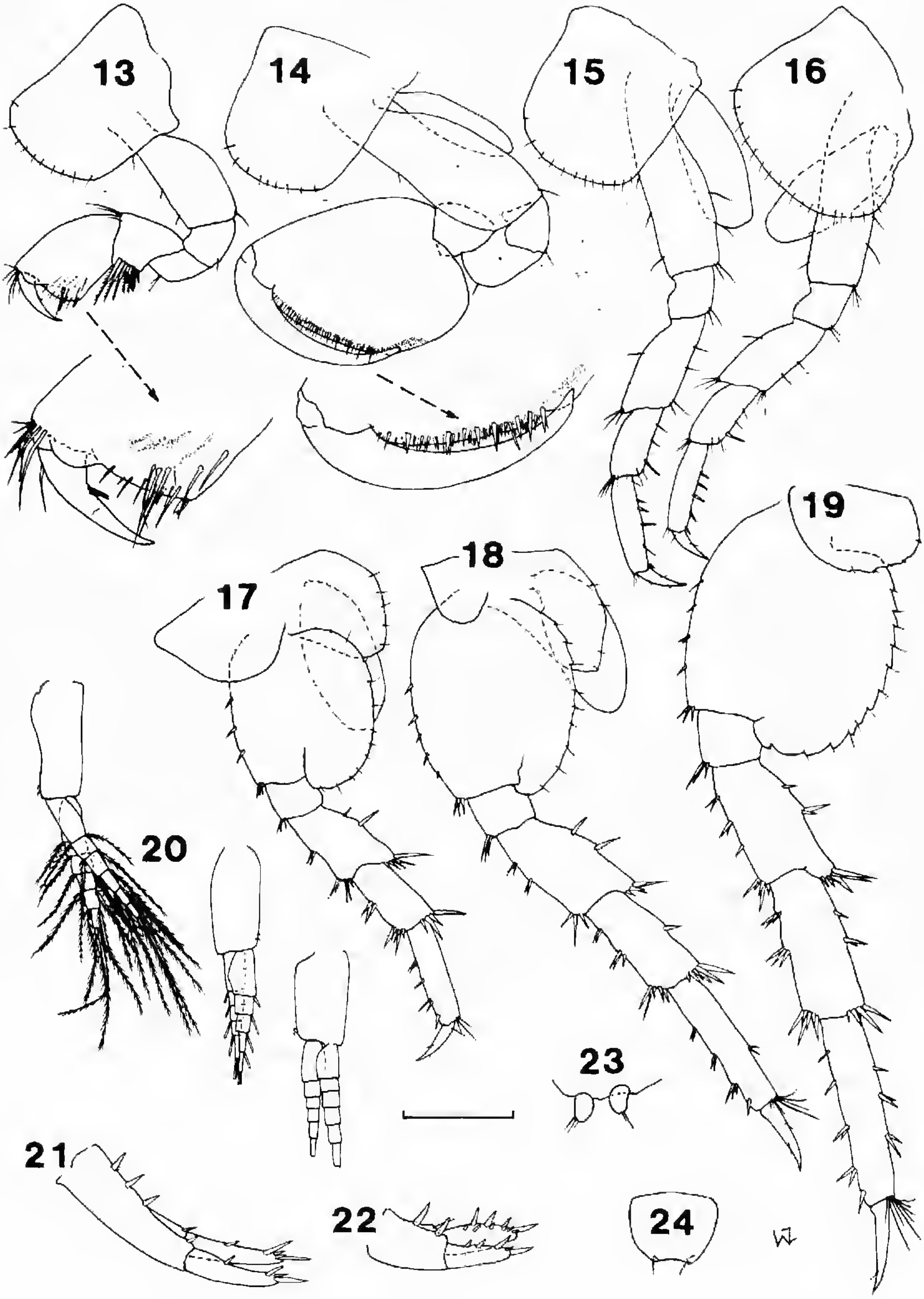
Maxilla 1 (Fig. 7): outer plate with nine comb-like spines apically; inner plate very narrow with two feathered spines apically.

Maxilla 2 (Fig. 8): outer plate slightly longer than inner, setal row restricted to apex; inner plate with one large seta on inner margin about 0.6 from base, setal row apically and along inner margin almost to large seta.

Maxilliped (Fig. 6): inner plate reaching extremity of article 1 of palp, rectangular, width about 3× length, with three stout teeth apically, the inner one



Figs 3-12, *Phreatochiltonia anophthalma* gen. et sp. nov., holotype ♂. 3, lateral view; 4, antenna 1; 5, antenna 2; 6, maxilliped; 7, maxilla 1; 8, maxilla 2; 9 & 10, mandible, left & right; 11, upper lip; 12, lower lip. Scale bars = 0.5 & 0.1 mm respectively.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smaller, few feathered setae apically and along inner margin; outer plate ovate, reaching 0.75 along article 2 of palp, slightly wider than inner plate, bearing several setae apically and along about distal ½ inner margin; palp article 1 with oblique distal margin, length outer margin about 2.5× inner; palp article 2 slightly broader than long, slightly expanded distally, as long as outer margin article 1, bearing group of setae on inner distal corner and along distal ⅔ inner margin; palp article 3 about as long as broad, slightly expanded distally, as long as article 2, bearing close-set setae on inner distal corner and for about distal ½ inner margin, several setae on outer distal corner and outer ⅓ distal margin; palp article 4 small, conical, width ⅔ length, slightly less than ½ article 3, four setae terminally; dactyl sharp, slightly longer than article 4.

Gnathopod 1 (Fig. 13): coxa width 0.8× length, slightly longer than article 2, anterodorsal and posterodorsal corners slightly produced, distinctly wider proximally, anterior margin little longer than posterior margin, distal margin evenly rounded with several evenly spaced setae; article 5 length about 1.2× maximum width, posterodorsal lobe with close-set row of eight stout, pectinate spines; article 6 trapezoid, half as long again as article 5, slightly wider distally, width about ⅔ length, posterodistal corner with two stout spines on either side of dactyl, several long setae on anterodistal corner and on posterodistal lobe, several small setae on distal margin; dactyl slightly shorter than width article 6, fitting neatly against palm.

Gnathopod 2 (Fig. 14): length about 1.4× G1, coxal gill length more than 3× width, little shorter than coxa; coxa slightly longer than wide, about 0.8× article 2, distinctly wider proximally, distal margin evenly rounded with several evenly spaced setae; article 4 with right-angled bend; article 5 small, without pectinate spines; article 6 little shorter than article 2, length anterior margin 1.2× maximum width, posteroproximal corner forming rounded lobe, palm oblique with numerous spines of varying lengths on either side of cutting edge followed by shallow groove for tip of dactyl; dactyl claw-like, as long as anterior margin article 6.

Pereopod 3 (Fig. 15): slightly longer than G2; coxal gill length 2.5× width, little shorter than coxa; coxa like that of G2 but slightly larger; article 4 length 2× width, about 0.5× article 2, anterodistal corner produced; article 5 length ⅔ article 4; article 6 about as long as article 4; dactyl length 0.5× article 6; all articles sparsely setose as illustrated.

Pereopod 4 (Fig. 16): slightly shorter than P3, otherwise identical except for coxa; coxa distinctly wider than long, wider distally, anterior margin straight, distal margin evenly rounded extending to small posterodistal lobe, posterior margin with slight indentation but without proximal excavation.

Perepod 5 (Fig. 17): length about 0.9× P4; coxal gill nearly twice as long as wide, as long as article 2; coxa width about 1.5× width article 2, length anterior lobe almost ½ width coxa, length posterior lobe 0.6× width coxa or 0.8× length article 2; article 2 slightly longer than wide with typical expanded posterior margin and posterodistal lobe reaching to about ½ article 3; article 4 length 1.3× width, ½ length article 2, with posterodistal corner produced; article 5 slightly longer than article 4, width about ½ length; article 6 length 1.3× article 5, width ¼ length; dactyl length about ½ article 6; all articles sparsely spinose as illustrated.

Pereopod 6 (Fig. 18): length 1.4× P5; like P5 except for coxa; coxa almost as wide as article 2, length anterior lobe ⅓ article 2, length posterior lobe ⅔ article 2 or 0.8 width coxa.

Pereopod 7 (Fig. 19): longest pereopod, length about 1.2× P6; like P6 except coxa is semi-circular and lacks coxal gill, width 1.4× length, and article 2 posterior margin is distinctly serrated above insertion of setae with acute proximal shoulder.

Pleopods (Fig. 20): all unmodified (c.f. *Chiltonia*).

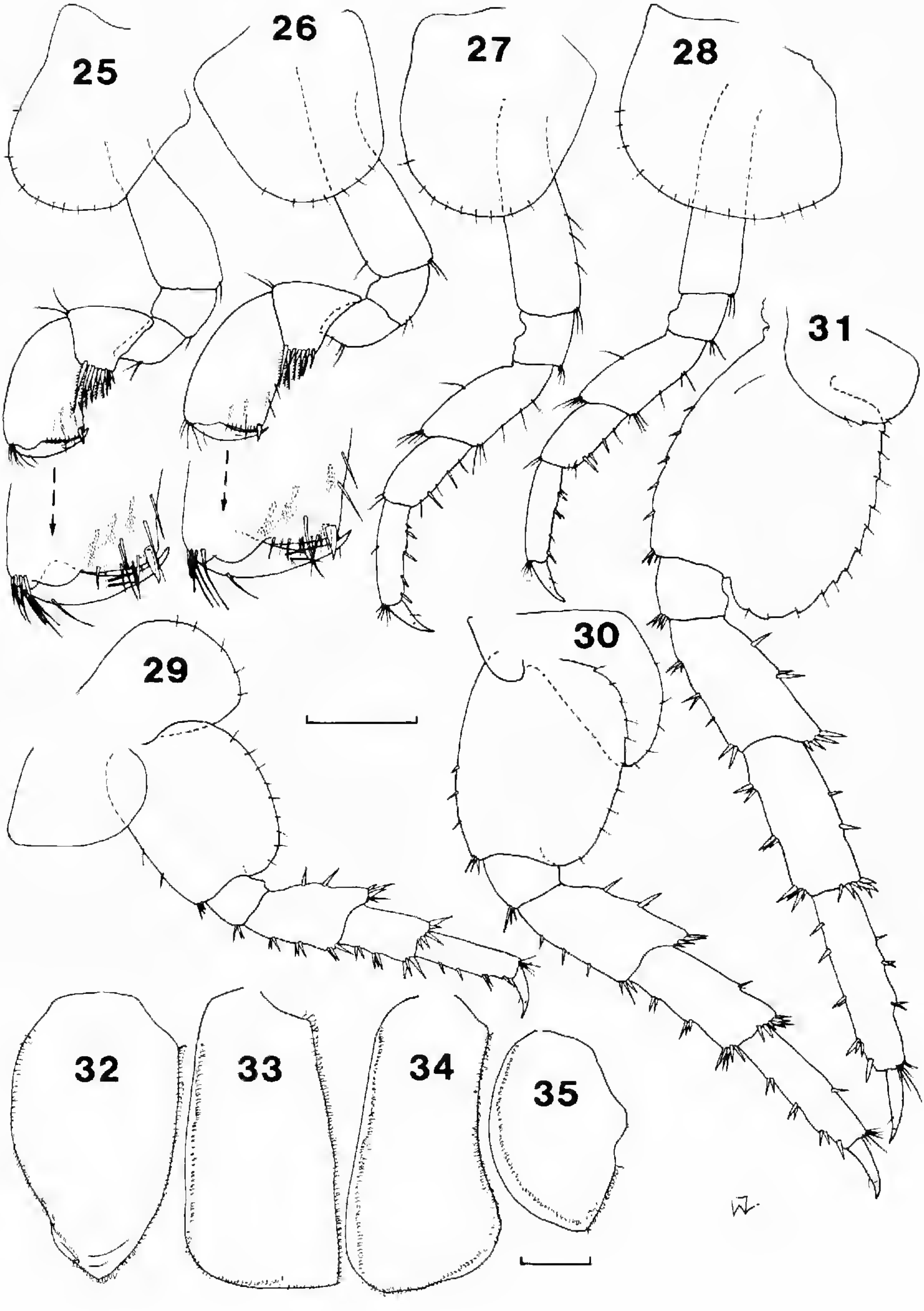
Uropod 1 (Fig. 21): length about 1.8× U2; peduncle with small spine on inner and outer distal corners, and three large spines on dorsal outer margin; rami equal in length, about ⅔ peduncle, outer ramus with two large and one small spine at tip and one large spine medially on dorsal margin; inner ramus with two large and two small spines at tip and one large spine medially on dorsal margin.

Uropod 2 (Fig. 22): peduncle with two large spines on dorsal margin, one medially, the other near distal corner; rami subequal, as long as peduncle, outer ramus with one large spine terminally, one small spine subterminally and three large spines on dorsal margin; inner ramus like outer but in addition a row of five small spines, adjacent to larger spines, on inner dorsal margin.

Uropod 3 (Fig. 23): one-articulate (rami absent), almost ½ length telson, rounded in cross-section with one (right) or two (left) outer and one short inner seta at tip.

Telson (Fig. 24): entire, subrectangular, length about ¾ width, distal margin slightly concave with two small setae at each corner.

Figs 13–24. *Phreatochiltonia anophthalma* gen. et sp. nov., holotype ♂, 13–19, gnathopods 1 & 2, pereopods 3–7; 20, pleopods 1–3 (feathered setae on 2 & 3 not shown); 21–23, uropods 1–3, 24, telson. Scale bar = 0.2 mm.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Description of allotype: Female 3.8 mm, ovigerous with 28 eggs in brood-pouch, like male except for the following.

Antenna 1: flagellum length 1.6× peduncle, of eight articles with one ventral aesthetasc at base of each of last three articles.

Antenna 2: flagellum length slightly more than 1.3× peduncle, of six articles.

Gnathopod 1 (Fig. 25): article 5, posterodistal lobe with close-set row of nine, stout, pectinate spines; article 6 more rectangular, width about 0.6× length, stout spines on posterodistal corner either side of dactyl slightly larger; dactyl a little longer than width article 6.

Gnathopod 2 (Fig. 26): like G1 but length about 1.2× G1, and article 5 posterodistal lobe with close-set row of seven, stout, pectinate spines.

Pereopod 3 (Fig. 27): length about 1.2× G2.

Pereopod 4 (Fig. 28): coxa slightly wider than in male, length only 0.8× width.

Pereopod 5 (Fig. 29): coxa slightly wider than in male, width about 1.8× width article 2; article 2 with small posterodistal lobe; article 4 slightly longer than article 5.

Pereopod 6 (Fig. 30) and pereopod 7 (Fig. 31): as for holotype, but article 2 slightly narrower and with very small posterodistal lobe in P6.

Oostegites (Figs 32–35): on coxae 2–5, all with curled margins and numerous small hooks, together forming tight marsupium. First is heart-shaped, slightly shorter than G2, length 1.8× maximum width; second is trapezoid, length 0.8× P3, 2.7× width proximally and 2× width distally; third is similar to second but with concave posterior margin; fourth is subovate with very convex anterior margin and oblique distal margin, length about 0.6× P5, 1.4× maximum width.

Pleopods, uropods and telson as in holotype.

Etymology: The specific name *anophthalma* refers to the absence of eyes.

Variation

Apart from variations due to size (e.g. number of flagellar articles of antennae), paratypes and other material examined was remarkably similar to either the holotype or allotype. Minor differences noted were as follows. The number of aesthetascs on A1 varies with some males having an additional one (five), and some females an additional one (four) or rarely two (five). In the male paratype (SAM C4330) and also the larger male paratype from the AM collections (AM P40445) G2 from the left is noticeably smaller than from the right, in all other specimens homologous pereopods are of similar size. The spination of U1&2 varied slightly with a few specimens with more or less spines (usually only one, at most two). In one specimen (female), from spring E8, U3 from the right is two-articulate (uniramous) as found in *Austrochiltonia australis* (Sayce, 1901). Oostegites of females vary considerably in size, but are expanded, as illustrated, in ovigerous specimens.

The possibility that speciation may have occurred between springs without any obvious morphological changes was considered, and specimens for allozyme electrophoretic analysis were collected from springs Db4 (type locality), E8 and Ga4. A preliminary analysis of this material using methods outlined by Richardson *et al.* (1986) indicated fixed genetic differences of less than 10% (for 16 loci), thus supporting the morphological evidence of one species with little variation. Given these results, a more detailed analysis was considered unnecessary.

Discussion

The new species described here closely resembles an undescribed species that I have collected from springs scattered throughout the Flinders Ranges in northern South Australia, sympatric with one or more undescribed Crangonyctoid species. However, this other species is not described here as considerably more work is required to determine whether or not one or more species are present.

Phreatochiltonia anophthalma has been found only in a few, relatively cold, seeps amongst the 100 or so springs and mounds known as Dalhousie Springs, most of which were sampled in 1985 (Zeidler & Ponder 1989). Many of the active springs at Dalhousie are warm (> 30°C) with large outflows (Smith 1989), and since freshwater amphipods prefer cooler waters (Barnard & Barnard 1983), it is not surprising that no phreatic amphipods were found in these springs. However, a species of *Austrochiltonia* was found in two of these warm springs, but only amongst sedges along the edges of outflows where the water was considerably cooler (Zeidler 1989).

The habitat of *P. anophthalma* is very restricted and animals were seen at the surface, burrowing in and out of the substrate, only near points of water discharge, or were found under plant debris nearby. The species was moderately abundant at most sites except springs Cb1 and E2, which had little or no surface water present. The habitat at the other sites

Figs 25–35, *Phreatochiltonia anophthalma* gen. et sp. nov., allotype ♀. 25–31, gnathopods 1 & 2, pereopods 3–7; 32–35, oostegites from coxa 2–5. Scale bar = 0.2 mm.

was very limited, consisting of small seeps about 3 m long by 20 cm wide, and only a few millimetres deep. At Cb1 one specimen was collected incidently with hydrobiid molluscs in May 1983, from a small shallow pool on the top of the mound. In 1985, this spring was completely dry, but two specimens were collected from a mop trap placed in a hole dug to the water level, adjacent to the mound. This evidence suggests that these amphipods are essentially subterranean in habit and are only seen at the surface when underground water pressure is sufficient to breach the surface of the mound. The notion that these animals, and perhaps others, inhabit the cool interstitial water beneath and between mounds is an interesting prospect that needs further investigation.

Factors that determine the distribution of this species are unknown, but since the habitat appears very limited, it may be more vulnerable to external influences than are the habitats of larger springs. Presence of surface water is probably unnecessary for the survival of the species (e.g. at Cb1), and on a brief visit in April 1986, all habitats had contracted, animals were difficult to collect, and half of the habitat of E8 had dried up. However when surface water is present, they may concentrate at the point of discharge.

Nothing is known about the life history of this species, but of the 366 females collected, 97 were ovigerous, and recently hatched juveniles were common.

One can only speculate as to the evolutionary origin of this species, but its occurrence at Dalhousie Springs on the edge of the Simpson Desert may indicate that it is a descendent of a species which was more widespread during a time when central Australia was much wetter than it is today (Krieg 1989). The phreatic habit having most likely evolved in response to selective pressures in an arid environment.

Acknowledgments

I am most grateful to Dr W. F. Ponder (AM), who dared to suggest that phreatic amphipods might exist at Dalhousie Springs, and who collected the first specimen in May 1983, provoking a more intensified search in 1985. He is also thanked for his assistance in the field and for collecting more specimens, as is Ms D. Winn (AM). Mrs K. L. Gowlett-Holmes (SAM) assisted greatly with field work and the collection of specimens, and also typed the manuscript. Mr M. Adams, Evolutionary Biology Unit, SAM, conducted the electrophoretic analysis, and his expertise is gratefully acknowledged. I also acknowledge constructive comments of an anonymous referee which markedly improved this paper.

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